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BIODIVERSITY RESEARCH

Population structure, propagule pressure, and conservation biogeography in the sub-Antarctic: lessons from indigenous and invasive springtails

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ABSTRACT

The patterns in and the processes underlying the distribution of invertebrates among Southern Ocean islands and across vegetation types on these islands are reasonably well understood. However, few studies have examined the extent to which populations are genetically structured. Given that many sub-Antarctic islands experienced major glaciation and volcanic activity, it might be predicted that substantial population substructure and little genetic isolation-by-distance should characterize indigenous species. By contrast, substantially less population structure might be expected for introduced species. Here, we examine these predictions and their consequences for the conservation of diversity in the region. We do so by examining haplotype diversity based on mitochondrial cytochrome *c* oxidase subunit I sequence data, from two indigenous (*Cryptopygus antarcticus travei*, *Tullbergia bisetosa*) and two introduced (*Isotomurus* cf. *palustris*, *Ceratophysella denticulata*) springtail species from Marion Island. We find considerable genetic substructure in the indigenous species that is compatible with the geological and glacialogical history of the island. Moreover, by employing ecological techniques, we show that haplotype diversity is likely much higher than our sequenced samples suggest. No structure is found in the introduced species, with each being represented by a single haplotype only. This indicates that propagule pressure is not significant for these small animals unlike the situation for other, larger invasive species: a few individuals introduced once are likely to have initiated the invasion. These outcomes demonstrate that sampling must be more comprehensive if the population history of indigenous arthropods on these islands is to be comprehended, and that the risks of within- and among-island introductions are substantial. The latter means that, if biogeographical signal is to be retained in the region, great care must be taken to avoid inadvertent movement of indigenous species among and within islands. Thus, quarantine procedures should also focus on among-island movements.

Keywords
Biological invasion, Collembola, conservation biogeography, mtDNA COI, rarefaction.

INTRODUCTION

The patterns in and processes underlying the distribution of invertebrates at broad scales across the Southern Ocean islands are now reasonably well understood. For indigenous species, richness is positively related to energy availability, with distance from source areas and host plant diversity also contributing to richness variation in some taxa (Chown *et al.*, 1998, 2005). Dispersal ability is a major determinant of patterns of distribution, with less vagile taxa showing affinities to biotas of the source areas lying closest to the islands they inhabit, and more mobile taxa providing evidence for an Insulantarctic province (Greve *et al.*, 2005; see also Muñoz *et al.*, 2004). For introduced species, both richness and patterns of occurrence are strongly related to energy availability and propagule pressure (Chown *et al.*, 2005; Frenot *et al.*, 2005). Overall, these patterns and the processes underlying them are largely in keeping with those found elsewhere (e.g. Kalmar & Currie, 2006; Stark *et al.*, 2006). Within-island distribution patterns of invertebrates have also been investigated on several islands (e.g. Davies, 1973; Vogel, 1985; Tréhen *et al.*, 1986; Chown, 1989, 1990; Chown & Klok, 2001; Barendse *et al.*, 2002; Hugo *et al.*, 2004). Two major biotopes can

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be distinguished on all of the sub-Antarctic islands. The older, epilithic biotope has a high species richness, and its inhabitants are relatively stenotopic and are thought to have survived at least the most recent glaciations. By contrast, the vegetated biotope is much younger and characterized by recent, eurytopic colonists (see also Marshall & Convey, 2004).

However, the extent to which populations in these major biotopes are further structured has received little attention. Given that, at least on the larger sub-Antarctic islands, the landscape was substantially dissected by major glaciers and probably by volcanic activity (Nougier, 1972; Mercer, 1983; Hall, 1990, 2002; McDougall *et al.*, 2001; Ruddell, 2006), and that the indigenous faunas are thought to be hundreds of thousands if not millions of years old (Grobler *et al.*, 2006; Stevens *et al.*, 2006a; Chown & Convey, 2007), substantial population structure should characterize the indigenous species. Owing to the idiosyncratic nature of the disturbances, isolation-by-distance (see Lowe *et al.*, 2004) should also be minimal. Certainly on the Antarctic continent, glaciation has played a major role in population structuring and speciation (Marshall & Coetzee, 2000; Fanciulli *et al.*, 2001; Frati *et al.*, 2001; Stevens & Hogg, 2003; Nolan *et al.*, 2006).

By contrast, substantially less population structuring should characterize the species introduced by humans to these islands. The large majority of introductions are probably recent, with many having taken place in the late 19th, and 20th centuries (Chown *et al.*, 2002; Frenot *et al.*, 2005), providing little time for population divergence (see Sakai *et al.*, 2001; Kumar, 2005). If only a few individuals were involved in the initial colonization event, then even less structure might characterize these species. Although propagule pressure is one of the most significant determinants of establishment success in a range of organisms (Williamson, 1996; Chown *et al.*, 1998; Duncan *et al.*, 2003; Lockwood *et al.*, 2005), even very small numbers of individuals can give rise to persistent populations (Memmot *et al.*, 1998; Grevstad, 1999; Forsyth & Duncan, 2001; Gaston *et al.*, 2003). Thus, populations of the introduced species should show almost no population structure despite significant landscape complexity.

In this paper we examine these predictions using two indigenous and two introduced springtail species from sub-Antarctic Marion Island. We pay special attention to the implications of our findings for conservation biogeography: the application of biogeography to problems regarding the conservation of biodiversity (Whittaker *et al.*, 2005). Specifically, we consider the consequences of these findings for understanding the relationships among populations (and species), the areas they inhabit across the Antarctic region (see Stevens *et al.*, 2006a) and their consequences for the establishment of invasive alien species and therefore for the control of inter-island and inter-area (including within-island) movement of humans in the broader Antarctic region.

MATERIALS AND METHODS

Marion Island (46°54′ S, 37°55′ E) is approximately 450,000 years old, and has experienced several glacial cycles and volcanic episodes, during which time its landscape was substantially subdivided (Hall, 1990, 2002; McDougall *et al.*, 2001). Glaciations took place at 10–35 ka, 40–87 ka, possibly at *c.* 110 ka, at 170–200 ka, probably at 240–300 ka and at 450–420 ka. Volcanism corresponds well with these dates and the two kinds of events are thought to be related. Volcanism is recorded from < 10 ka (minor flows as recent as 2 years ago), 20–70 ka, 85 ka, 110 ka, 156–201 ka, 244 ka, 323–363 ka and 454–413 ka (McDougall *et al.*, 2001). At the height of many of the previous glaciations, large areas were covered by ice. In consequence, it seems likely that during the glacial maxima, populations of invertebrates and plants were substantially reduced in size (see Chown, 1990), and may well have been isolated. Although the role of volcanism in causing isolation is less clear, recent interpretations suggest that many of the valley landforms and scarps on the island are the result of volcanic eruptions (Boelhouwers *et al.*, 2007).

Sixteen Collembola species have been recorded from Marion Island (Chown *et al.*, 2002). Of these, 10 are indigenous and widely distributed around the island, showing some preference for the older, drier fellfield areas (Gabriel *et al.*, 2001; Hugo *et al.*, 2006). The other six introduced species are also abundant around the island at lower elevations (except for *Pogonognathellus flavescens*, which is a more typically eastern coastal species) (Gabriel *et al.*, 2001; Hugo, 2006). With one exception, they are thought to have been introduced by humans at least by the early 1970s (Deharveng, 1981), but most likely during the importation of fodder for sheep kept at the island station in the 1950s (Cooper & Condy, 1988).

The indigenous springtail species *Cryptopygus antarcticus travei* Deharveng (Isotomidae) (which is likely a species in its own right, see Stevens *et al.*, 2006a) and *Tullbergia bisetosa* Börner (Onychiuridae), and the introduced species *Isotomurus* cf. *palustris* Müller (Isotomidae) and *Ceratophysella denticulata* Bagnall (Hypogastruridae) were used as exemplars for this study. They were collected by sieving and aspiration from mosses and other plant material from around the island (Table 1; Fig. 1). All individuals were preserved in absolute ethanol.

DNA amplification and sequencing

Total genomic DNA was extracted using standard procedures described in Maniatis *et al.* (1982). Standard polymerase chain reactions (PCR) were set up (see Mortimer & Jansen van Vuuren, 2006) to amplify a fragment of the COI gene using the primer combination LCO1490 and HCO2198 (Folmer *et al.*, 1994). Amplicons were directly cycle sequenced using BigDye chemistry (version 3, Applied Biosystems, Fairlands, South Africa). All sequencing reactions were performed with the primer LCO1490. However, to verify our sequence data as well as to complete missing data, sequences were also generated with the primer HCO2198. Unincorporated dye label was removed by sephadex columns before the samples were run on an ABI 3100 automated sequencer (Applied Biosystems). Electropherograms were checked using Sequence Navigator (ABI, version 1.01) and aligned by eye. Sequences were submitted to GENBANK (accession numbers DQ147289–DQ147558 and EF051625).

Table 1 Numbers of individuals of each species collected at each sampling locality on Marion Island

Locality name	Latitude	Longitude	Altitude (m)	C.ant	T.bis	I.pal	C.den
Trypot (1)	46°53′05″ S	37°52′05″ E	13	*	*	8	5
Skua Ridge (2)	46°52′04″ S	37°50′17″ E	88	*	*	4	*
Swartkop Point (3)	46°55′28″ S	37°35′44″ E	57	9	5	9	*
Kildalkey Bay (4)	46°58′01″ S	37°31′10″ E	19	11	5	9	4
Blue Petrel Bay (5)	46°50′48″ S	37°49′06″ E	33	*	5	11	*
Ship's Cove (6)	46°51′14″ S	37°50′30″ E	30	5	*	*	*
Fred's Hill (7)	46°54′49″ S	37°50′21″ E	230	*	*	5	*
Hendrik Vister Kop (8)	46°53′12″ S	37°48′49″ E	282	10	5	*	*
Katedraalkrans (9)	46°53′54″ S	37°46′29″ E	768	5	3	*	*
Long Ridge (10)	46°52′55′ S	37°47′11′ E	515	5	*	*	*
Archway Bay (11)	46°53′56″ S	37°53′42″ E	39	10	2	8	7
Greyheaded Albatross Ridge (12)	46°57′43″ S	37°42′31″ E	84	7	*	*	*
Mixed Pickle (13)	46°52′20″ S	37°38′21″ E	50	*	4	5	*
Cape Davis (14)	46°49′41″ S	37°42′14″ E	63	6	5	*	*
Rook's Bay (15)	46°58′01″ S	37°39′39″ E	67	*	3	*	*
Stony Ridge (16)	46°55′03″ S	37°51′31″ E	162	7	*	*	*
Mesrug (17)	46°56′37″ S	37°50′52″ E	141	*	3	*	*
Bullard (18)	46°55′16″ S	37°52′53″ E	42	*	*	6	3
Base (19)	46°52′56″ S	37°51′63″ E	14	*	*	*	7
Watertunnel Stream (20)	46°58′30″ S	37°45′03″ E	64	*	*	*	7
Total				75	40	65	33

C.ant, *C. antarcticus travei*; T.bis, *T. bisetosa*; I.pal, *Isotomurus* cf. *palustris*; C.den, *C. denticulata*. * = no specimens.

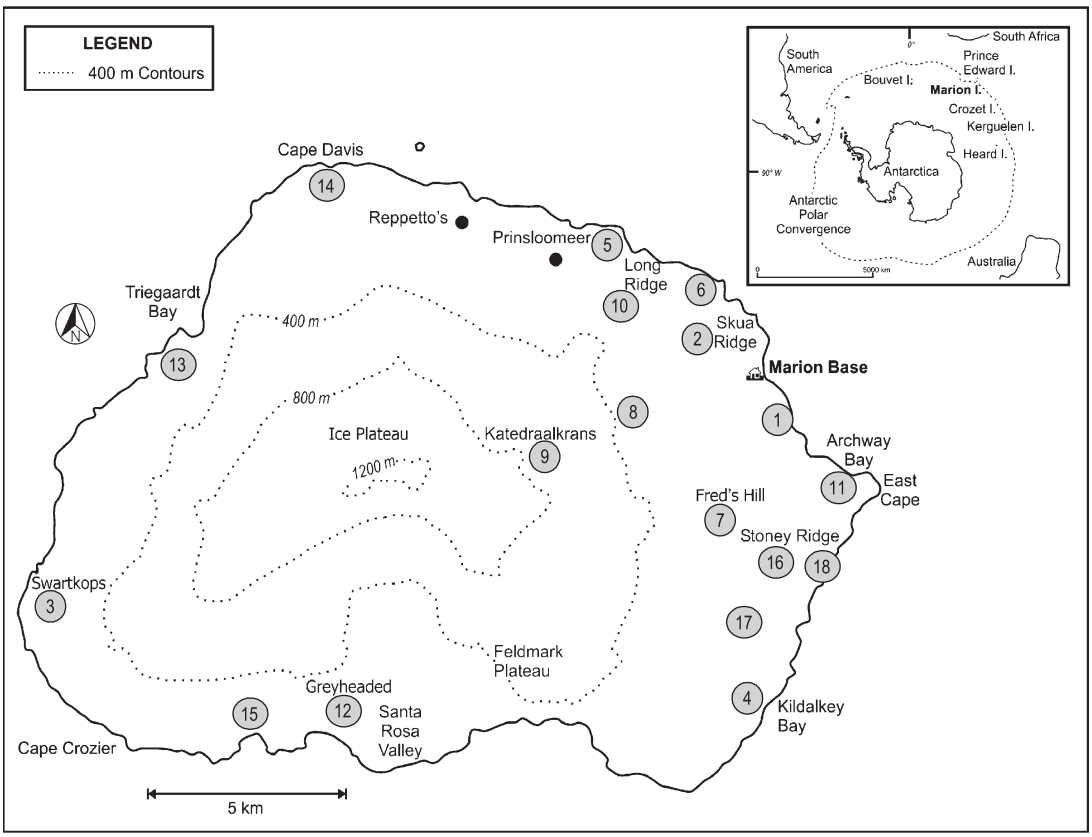

Figure 1 Map of Marion Island showing major geographical features and collection sites. Numbering corresponds with locality numbers provided in Table 1.

Data analyses

The number of variable and parsimony-informative sites and uncorrected p-distances separating specimens were determined using PAUP* (Swofford, 2000). Both intrapopulation divergences (uncorrected p-distances) and interpopulation divergences were calculated. The latter was corrected for ancestral polymorphisms following Nei & Li (1979), using the equation $d_A = d_{XY} - [(d_X + d_Y)/2]$, where d_{XY} = divergence between populations X and Y and d_X and d_Y = intraspecific divergence within population X and Y, respectively. ARLEQUIN (version 3, Excoffier *et al.*, 2005) was used to calculate haplotype diversities.

In a departure from traditional approaches, but in keeping with Lowe *et al.*'s (2004: 66) suggestion that rarefaction techniques can be used to estimate haplotype diversity, ecological methods were also used to estimate the extent to which the majority of haplotypes had been sampled and how many haplotypes might exist in the populations. Specifically, the non-parametric Chao 2 and Jacknife 2 estimators were calculated and an individual-based rarefaction curve (see Gotelli & Colwell, 2001; Magurran, 2004) was constructed for each of the species using the ESTIMATES vs. 7.51 software (Colwell, 2005). These methods have traditionally been applied either for estimating the likely total species richness of a given habitat based on sampling data, or for comparing richness values among habitats or sampling periods for a given number of samples or individuals (Magurran, 2004). From the species richness perspective, the theory underlying and performance of these methods is being increasingly well explored (e.g. Brose *et al.*, 2003; Brose & Martinez, 2004; Chao *et al.*, 2005; O'Hara, 2005; Ulrich & Ollik, 2005; Walther & Moore, 2005). However, the methods are not commonly applied to haplotype data. We did so, making the explicit assumption that the theory underlying the sampling of haplotypes within a population is sufficiently similar to the theory underlying the sampling of species within assemblages to provide a reasonable estimate of the haplotype diversity and the extent to which this had been sampled. Individual-based rarefaction curves were used because our sampling unit was individuals (Gotelli & Colwell, 2001), and the Chao 2 and Jacknife 2 estimators adopted because they are generally most robust (Brose *et al.*, 2003; Walther & Moore, 2005). For comparative purposes, we also constructed a hypothetical matrix for a sample of 80 individuals consisting of 25 haplotypes in which all haplotypes were likely to have been well sampled (i.e. few unique haplotypes).

To investigate the level of connectedness among populations, minimum spanning trees were constructed by hand using distances (mutational steps separating haplotypes) obtained from ARLEQUIN. A more demographic approach was also adopted where the spatial distribution of mitochondrial variation was explored using a spatial analysis of molecular variance (SAMOVA, Dupanloup *et al.*, 2002). This approach maximizes population genetic structure and, as a consequence, allows the inference of possible geographical barriers to gene flow between these inferred groups. Conventional Φ statistics were calculated in ARLEQUIN and 1000 randomizations were used to provide null models for these statistics.

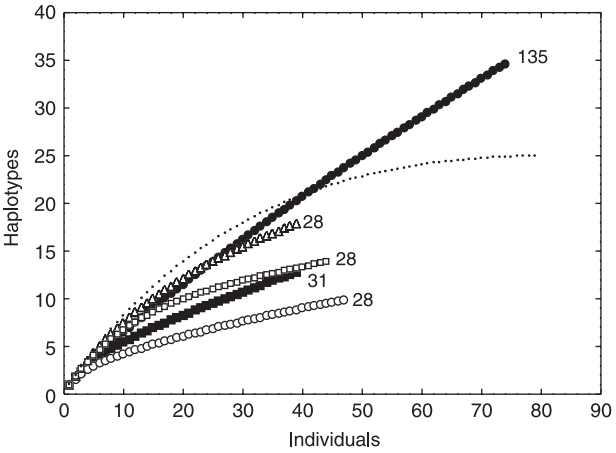

Figure 2 Individual-based rarefaction curves illustrating the increase in the number of haplotypes with increasing numbers of individuals. The numbers next to the curves indicate the total estimated number of haplotypes using the non-parametric Chao2 estimator. The finely dotted line represents a hypothetical population sampled to completion. The remainder of the lines are: ● *C. antarctics travei*, ■ *T. bisetosa*, ○ *G. hodgsoni* (data from Nolan *et al.*, 2006), □ *G. hodgsoni* (data from Stevens & Hogg, 2003), △ = *D. klovstadi* (data from Frati *et al.*, 2001).

A Mantel test for isolation-by-distance was performed using ARLEQUIN. Longitudinal and latitudinal coordinates were converted into geographical distances and compared to the observed genetic distances between different populations. It was reasoned that the springtails would cross the island by circumventing the stationary glacier (or ice plateau) that is typical of the island above *c.* 1000 m (Van Zinderen Bakker *et al.*, 1971; Sumner *et al.*, 2004) rather than by traversing it. Thus, distances were not always calculated as straight-line measurements but rather followed hypothetical colonization routes available to the invertebrates.

RESULTS

Indigenous species

Cryptopygus antarcticus travei

Six hundred and ten base pairs of the COI gene were amplified and sequenced from 75 individuals collected from 10 localities (Table 1; Fig. 1). Of these, 51 characters were variable and 19 parsimony informative. From the 75 specimens analysed, 35 different haplotypes were identified. Although several specimens shared haplotypes, many private/unique haplotypes were observed (29 singletons) and this is reflected in the relatively high haplotype diversity of 0.91. The estimators indicated that many more (89–135) haplotypes are likely to be present in this species and that sampling was far from complete (Fig. 2). The most common haplotype characterized 32 specimens and is widespread across the island. The highest uncorrected p-distance separating specimens was

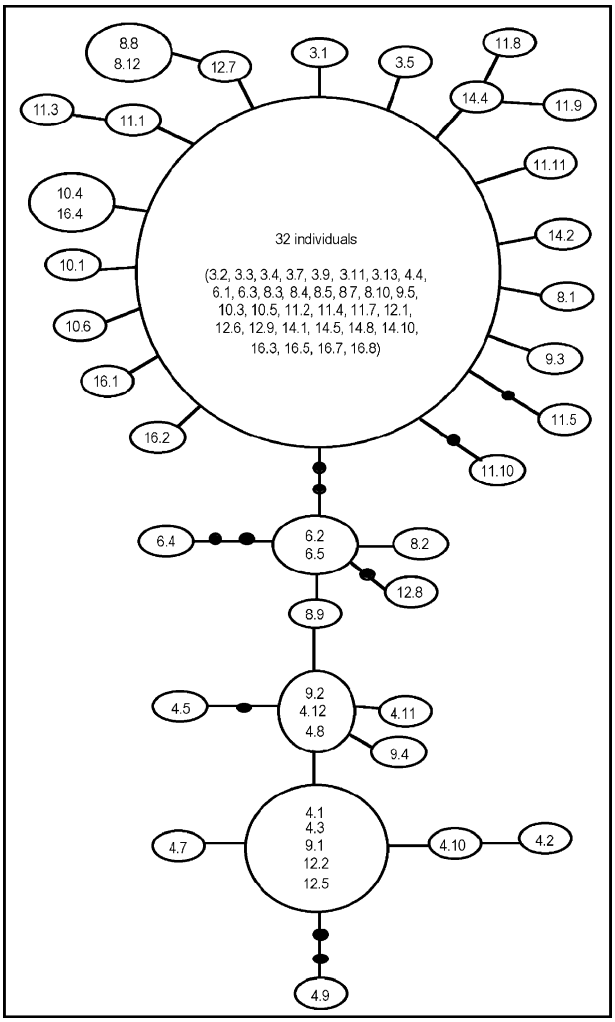

Figure 3 A minimum spanning tree based on 610 bp of COI for 75 *C. antarcticus travei* individuals. Lines separating haplotypes represent one mutational difference between them and missing haplotypes are indicated by filled circles. Specimen numbers in the network are identified by two numbers; the first is the locality number (see Table 1) and the second the specimen number from each respective sampling locality.

2.94% between individuals sampled at Archway Bay and Grey-headed Albatross Ridge.

A minimum spanning tree (Fig. 3) was drawn by hand using the least number of mutational steps separating haplotypes (see Discussion by Cassens *et al.*, 2005 of optimal network selection). Two distinct demographic signatures were evident: the first resembles a star-like pattern with the majority of specimens (32) sharing a single haplotype. Several haplotypes separated by only one or two nucleotide differences are derived from this central haplotype. The second signature, seen in the lower section of the tree, is characterized by higher numbers of nucleotide differences separating haplotypes with fewer shared haplotypes.

When considering sampling localities as populations, AMOVA indicated that the largest portion of the variance (72.5%) was attributable to variation within different populations, with the remainder (27.5%) a consequence of variation between populations. Despite the variability within populations, the Φ_{ST} value was significant (0.27; $P < 0.001$). Population pairwise Φ_{ST} comparisons indicated that many of the populations differed significantly (Table 2). For example, Kildalkey Bay differed significantly from eight other populations and Swartkop Point from seven.

On average, the corrections for ancestral polymorphisms reduced divergences by 0.48% (Table 2). The highest intra-population divergence was 0.78%, recorded for Katedraalkrans, which is a high elevation site (*c.* 768 m) located on the eastern side of the island. The largest (corrected) sequence divergence between populations was 0.65% between Kildalkey Bay and Long Ridge. Spatial analyses of molecular variation (SAMOVA) returned Φ_{CT} values that were significant ($P < 0.001$) for all group numbers specified, except for the category with two groups. The Φ_{CT} value was maximized when five groups were specified (0.37, $P < 0.001$). Kildalkey Bay remained distinct irrespective of the number of groups selected. The Mantel test was not significant ($P = 0.58$) indicating no isolation-by-distance for *C. antarcticus travei* based on the COI data set.

Tullbergia bisetosa

Forty *T. bisetosa* specimens were included from 10 localities distributed across Marion Island (Table 1; Fig. 1). In total, 606 bp were analysed, 22 of which characters were variable and 8 were parsimony informative. Thirteen haplotypes were identified, which included nine singletons. The three most common haplotypes characterized 15, 7 and 7 specimens, respectively. Haplotype diversity was high at 0.900. The estimators suggested, again, that more (29–31) are present than were sampled, and that sampling had not gone to completion (Fig. 2). The minimum spanning tree (Fig. 4) is dominated by the three haplotypes, with specimens possessing these haplotypes are widespread across the island.

The highest uncorrected p-distance separating specimens was 1.73% between specimens collected at Rook's Bay and Mesrug. On average, the corrections for ancestral polymorphisms reduced differences by 0.48% (Table 3). The highest intra-population divergence was 0.79% recorded for Mesrug. The largest (corrected) divergence between populations was 0.43% between Kildalkey Bay and Hendrik Vister Kop.

When considering sampling localities as populations, AMOVA indicated that the largest portion of the variance (86.2%) can be attributed to variation within different populations with the remainder (13.8%) a consequence of variation between populations. The Φ_{ST} value was significant (0.14; $P = 0.036$), and population pairwise Φ_{ST} comparisons (Table 3) indicated that Kildalkey Bay differed significantly from four other populations. Katedraalkrans, the high altitude locality included in the present study, did not differ significantly from any of the localities and in fact, had not diverged at all from the majority of localities.

Spatial analyses of molecular variance (SAMOVA) yielded Φ_{CT} values that were low, sometimes negative and never significant irrespective of how many groups were specified. This may be the result of relatively small sample sizes included for the different

Table 2 Pairwise population $_{ST}$ values based on 610 bp of COI for 75 *C. antarcticus travei* specimens indicated above the diagonal

	Swartkops	Kildalkey	Hendrik Vister	Katedraal	Cape Davis	Ship's Cove	Archway Bay	Grey-headed	Long Ridge	Stony Ridge
Swartkops	0.223	0.504*	0.056	0.387*	0.295*	0.336	0.115*	0.213*	0.092*	0.206*
Kildalkey	0.522	0.665	0.339*	0.079	0.540*	0.194*	0.505*	0.161*	0.501*	0.549*
Hendrik Vister	0.014	0.355	0.575	0.129	0.109	0.054	0.117*	0.010	0.044	0.109
Katedraal	0.185	0	0.050	0.799	0.408*	0.027	0.309*	0	0.327	0.415*
Cape Davis	0.005	0.610	0.037	0.266	0.180	0.410*	0.036	0.178	0.011	0
Ship's Cove	0.228	0.153	0.111	0	0.130	0.684	0.305*	0	0.350*	0.431*
Archway Bay	0.017	0.710	0.096	0.275	0.018	0.372	0.550	0.203*	0.014	0.056
Greyheaded	0.094	0.121	0.002	0	0.125	0.025	0.209	0.695	0.149	0.204
Long Ridge	0	0.648	0.043	0.278	0.007	0.339	0.025	0.141	0.313	0
Stony Ridge	0.025	0.629	0.043	0.265	0.006	0.328	0.004	0.146	0	0.265

*denotes comparisons for which $P < 0.05$. Pairwise differences separating localities, corrected for ancestral polymorphisms, are shown below the diagonal. Average pairwise differences within localities are indicated in the diagonal.

Table 3 Pairwise population Φ_{ST} values based on 606 bp of COI for 40 *T. bisetosa* specimens indicated above the diagonal

	Swartkops	Kildalkey	Hendrik Vister	Katedraal	Archway	Blue Petrel	Rook's	Mixed Pickle	Cape Davis	Mesrug
Swartkops	0.564	0.334	0.019	0	0.190	0	0.184	0	0.046	0.148
Kildalkey	0.195	0.133	0.657*	0.092	0.539*	0.346	0.092	0.324*	0.437*	0.383
Hendrik Vister	0.007	0.427	0.314	0.285	0.438	0.017	0.476*	0.067	0.128	0.301*
Katedraal	0	0	0	0.537	0	0	0	0	0	0
Archway	0.125	0.173	0.253	0.024	0.381	0.136	0	0.111	0.055	0
Blue Petrel	0	0.162	0.015	0	0.144	0.423	0.161	0	0	0.555
Rook's	0.028	0	0.306	0	0.001	0.050	0.730	0.041	0.192	0.029
Mixed Pickle	0	0.083	0	0	0.056	0	0	0.605	0	0
Cape Davis	0.029	0.251	0.069	0.001	0.089	0	0.063	0	0.627	0
Mesrug	0.044	0.116	0.117	0	0	0.014	0	0	0	0.793

*denotes comparisons for which $P < 0.05$. Pairwise differences separating localities, corrected for ancestral polymorphisms, are shown below the diagonal. Average pairwise differences within localities are indicated in the diagonal.

populations. The Mantel test was not significant ($P = 0.774$), indicating no genetic isolation-by-distance.

Introduced species

In *Isotomurus* cf. *palustris*, a 480-bp fragment was sequenced for 65 specimens from nine localities across Marion Island (Table 1; Fig. 1). No polymorphisms were found in this region and only a single haplotype was detected across the entire island. For *C. denticulata*, 646 bp were sequenced for 33 specimens from six localities across the island (Table 1; Fig. 1). Again, only a single haplotype characterized all specimens.

DISCUSSION

Although we predicted that haplotype diversity might be high in the indigenous species and low in those introduced to the island, the difference between the two groups of species was far more dramatic than we had anticipated. Although investigation of the indigenous species provided estimates of approximately 35–135 (*C. antarcticus travei*) and 13–31 (*T. bisetosa*) haplotypes, neither of the introduced species showed evidence of more than a single haplotype. Moreover, both the high diversity levels in the indigenous species and the low levels in the introduced ones are substantially different from those typically found in other springtail species from the region (e.g. Frati *et al.*, 2001; Stevens & Hogg, 2003; Nolan *et al.*, 2006; Stevens *et al.*, 2006a). Therefore, both require explanation.

Indigenous species

In the indigenous species, upper estimates of the number of haplotypes present ranged from 31 to 135 and, at least in the case of *C. antarcticus travei*, would seem likely to be substantially higher than the 28 haplotypes estimated for the Antarctic *Gomphiocephalus hodgsoni* studied by Stevens & Hogg (2003) and by Nolan *et al.* (2006), and the 28 haplotypes estimated for the Antarctic *Isotoma klovstadi* (now *Desoria klovstadi*, see Stevens *et al.*, 2006b) examined by Frati *et al.* (2001) (Fig. 2). Indeed, rarefaction showed that even with relatively low numbers of individuals,

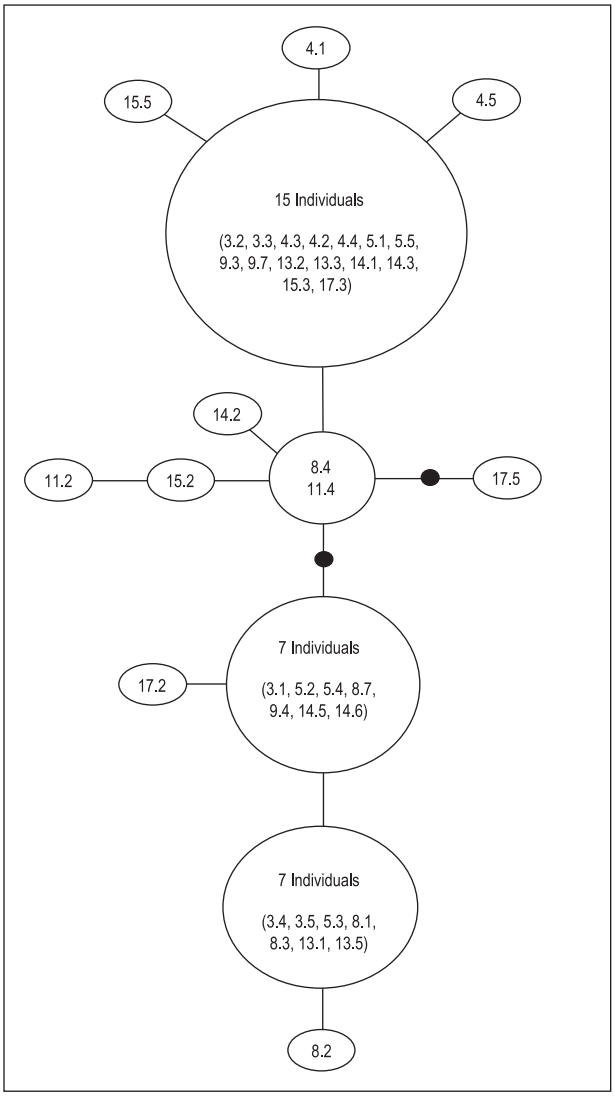

Figure 4 A minimum spanning tree based on 606 bp of COI for 40 *T. bisetosa* individuals. Lines separating haplotypes represent one mutational difference between them, and missing haplotypes are indicated by filled circles. Specimen numbers in the network are identified by two numbers; the first is the locality number (see Table 1) and the second the specimen number from each respective sampling locality.

C. antarcticus travei has substantially greater numbers of haplotypes than the other species. This high diversity might be accounted for in two major ways. If it is assumed that the COI marker is neutral, as is often done (Peek *et al.*, 2000), high diversity might reflect substantial within-island disjunction of populations. Alternatively, if the marker is not neutral, it might reflect some form of selection which has differentially affected certain groups of haplotypes (see Ballard & Rand, 2005). At present, no evidence is available for the latter alternative. Therefore, it is assumed that the marker is neutral (or nearly so) and the data are interpreted in that light.

Marion Island has a complex history of both volcanism and glaciation. Over the past 450,000 years eight major episodes of eruption and five large glacial episodes have affected the island's landscape (McDougall *et al.*, 2001). At least during the last glacial maximum, most of the island was covered by glaciers, although a few areas on the west and east coasts, as well as high elevation areas such as Feldmark Plateau, parts of Long Ridge and Katedraalkrans may have remained as refugia (Hall, 2002; Boelhouwers *et al.*, 2007). Conditions at this time are likely to have promoted population divergence as a consequence of vicariance. Moreover, geological and geomorphological evidence suggests that volcanism led to the formation of substantial valleys and ridges which may also have resulted in vicariance (Hall, 2002).

Although incomplete sampling is likely to bias interpretation of the molecular evidence to some extent (Morando *et al.*, 2003), the sequence data can be used to determine whether frequent vicariance is at least plausible and compatible with the geological evidence. To do so, we applied a molecular clock to our data. Despite the problems in using molecular clocks to estimate divergence times between organisms (Alroy, 1999; Lee, 1999; Conroy & Van Tine, 2003; Graur & Martin, 2004), no alternative exists in the absence of reliable fossil data. Therefore, following Soto-Adames (2002) a molecular rate of 2.3% per million years was applied to the COI data. In *C. antarcticus travei*, the oldest divergence time between populations is approximately 282,600 years (0.65% corrected sequence divergence) between Kildalkey Bay and Long Ridge, both of which are localities on the eastern side of the island. The date corresponds with glacial activity at oxygen isotope stage 8 (McDougall *et al.*, 2001). Other divergence times for *C. antarcticus travei* include a 227,000-year-old separation (0.52% corrected sequence divergence) between Swartkop Point and Kildalkey Bay, which is close to the dates of major glacial and volcanic events. These localities were also significantly differentiated from more than 50% of other localities based on pairwise Φ_{ST} values (Table 2), and, importantly, they were similarly distinct in the mite *Eupodes minutus* (Mortimer & Jansen van Vuuren, 2006). In *T. bisetosa*, fewer populations were significantly differentiated with only Kildalkey Bay and Hendrik Vister Kop, both situated on the eastern side of the island, differing from four and three populations, respectively. The molecular clock approach indicated that the Kildalkey Bay and Hendrik Vister populations have been separated for ~185,000 years (0.43% corrected sequence divergence), a time of major volcanic activity (McDougall *et al.*, 2001). Separation times between several populations also date to the last glacial maximum between 13,000 and 19,000 years ago (e.g. Hendrik Vister and Swartkop Point as well as Archway Bay and Swartkop Point in *C. antarcticus travei* and Hendrik Vister and Blue Petrel Bay as well as Mesrug and Blue Petrel Bay in *T. bisetosa*). Although only approximate, these dates correspond reasonably well with major periods of volcanism or glaciation on Marion Island (McDougall *et al.*, 2001).

Further evidence for the effects of glaciation comes from the Katedraalkrans populations of both indigenous species. This site is a high elevation one (*c.* 750 m a.s.l.), and is thought to have escaped the glaciation that was so characteristic of high elevation areas during the last glacial maximum (Boelhouwers *et al.*, 2007; I. Meiklejohn, personal communication). In *C. antarcticus travei* and *T. bisetosa* few of the populations are significantly differentiated from this locality, and the Katedraalkrans site had the highest

intrapopulation variability for the former species and nearly so for the latter (only marginally less than for Mesrug). High levels of intrapopulation variation are typical of what might be expected from a refuge population from which individuals have subsequently recolonized other areas (Jansen van Vuuren & Robinson, 1997; Hewitt, 2000), supporting the contention that Katedraalkrans was a major refugium.

Finally, in the absence of vicariant events, isolation-by-distance might be expected as populations slowly diverge from each other (Lowe *et al.*, 2004). Alternatively, with introgression following one or two events this might also be expected. However, isolation-by-distance was not typical of these species. Therefore, overall, the molecular data suggest that high haplotype diversity is a consequence of substantial within-island differentiation associated with historical subdivision of the landscape. Such intraisland differentiation has been found or suspected for other taxa both on these sub-Antarctic islands (Grobler *et al.*, 2006; Mortimer & Jansen van Vuuren, 2006) and elsewhere (Paulay, 1985; Otte, 1989; Gillespie & Roderick, 2002; Gillespie, 2004; see also Wagner & Funk, 1995).

A further notable feature of the data on haplotype diversity is that for both species Kildalkey Bay emerged as a locality substantially different to most other sites (see data on pairwise Φ_{ST} values). Almost without fail, SAMOVA analyses for both *C. antarcticus travei* and *T. bisetosa* also singled out Kildalkey Bay as distinct from the other sites (irrespective of the number of groups defined). This locality was similarly found to be distinct for the mite species *Eupodes minutus* (Mortimer & Jansen van Vuuren, 2006). Why this might be the case is not yet clear, but two hypotheses seem plausible. First, models of natural colonization of the island have suggested that wind-borne propagules are likely to be deposited in the lee of the island, which, given the prevailing north-westerly winds, is in the Kildalkey Bay region (Chown & Avenant, 1992). Furthermore, oceanic eddies in the wake of the islands could lead to deposition of material in this area (Froneman *et al.*, 1999), although the physical oceanographic setting of the islands is complex (Ansorge & Lutjeharms, 2002). Although the extent to which springtails might survive in the aerial plankton or in sea-water has not been fully assessed, several studies have indicated that such transport is plausible, and survival may be for a period long enough to enable colonization (Greenslade *et al.*, 1999; Coulson *et al.*, 2002). In addition, evidence for substantial *trans*-oceanic dispersal by a range of organisms is increasing (De Queiroz, 2005). Thus, Kildalkey Bay might represent a site of first colonization, and the arrival there in the last few decades of several species new to the island supports this idea (Chown & Avenant, 1992; Le Roux, 2007).

Alternatively, transport of springtails may have been by sealers who visited the island in the late 19th and early 20th centuries (Cooper & Headland, 1991; Cooper, 2007). Kildalkey Bay and other beaches close to it are known to have been used as sites by sealers during their visits to Marion Island. In addition, sealing ships often visited more than a single island on their voyages (Downes, 2002). In consequence, sealers may well have contributed to the distribution of small organisms around the region. Indeed, the data we collected on the springtail species known to have been introduced by humans from the Palaearctic to Marion Island suggest that introductions of only a small number of individuals might guarantee establishment (see below). Therefore, such interisland transfer was probably straightforward, especially if large amounts of cargo or terrestrial ballast were being exchanged. Moreover, the transfer of larger species between islands in the Southern Ocean region has been documented (e.g. Dreux *et al.*, 1992; Ernsting, 1993; Frenot *et al.*, 2005).

The fact that *C. antarcticus travei* is readily distinguishable from other *C. antarcticus* 'species' from elsewhere in the region (Stevens *et al.*, 2006a) suggests that this 'introduction hypothesis' is the least plausible of the two. However, Stevens *et al.* (2006a) commented on the substantial haplotype variability in the group, and noted that they had sequenced only five individuals of *C. antarcticus travei*. Given the substantial diversity we have found in this species the use of additional sequences might well alter the phylogeographical conclusions reached by Stevens *et al.* (2006a). Whatever, the outcome, substantial population structure and high haplotype diversity demonstrate that considerably greater sampling efforts may be required to fully understand the phylogeography of Southern Ocean island arthropods.

Introduced species

Although both of the introduced species studied here have been present on Marion Island at least since the late 1970s (Deharveng, 1981), they were each characterized by a single haplotype only. This suggests either that only a few individuals initially colonized the island, if the COI marker is neutral, or perhaps that some haplotypes were better able to cope with the abiotic conditions of the island (if the marker is influenced by the thermal environment — see Ballard & Rand, 2005). The latter hypothesis seems implausible given that low haplotype diversity is characteristic of several other invasive alien insect species too (e.g. Argentine ants, Tsutsui *et al.*, 2000; spiny waterfleas, Colautti *et al.*, 2005; guppies, Lindholm *et al.*, 2005). In consequence, it must be assumed that the founding populations were very small.

If the introduction of only a small number of individuals has led to the establishment of large populations of these springtail species (abundances may be as high as several thousand individuals per m^2, Gabriel *et al.*, 2001), propagule pressure is unlikely to have been a significant a factor in the establishment of these species, and perhaps for the group as a whole (for discussion of propagule pressure see Williamson, 1996; Lockwood *et al.*, 2005). In consequence, and assuming that climatic barriers are unimportant (see Richardson & van Wilgen, 2004 for a discussion of barriers to invasion), few hurdles to the introduction and establishment of small species such as these probably exist, as has been suggested previously both for this region and elsewhere (Lawton & Brown, 1986; Gaston *et al.*, 2003). Therefore, not only could further introductions from continental areas readily take place, but interisland transfers of indigenous species also seem likely. Following the cessation of sealing in the region (Cooper & Headland, 1991; Downes, 2002; Chown *et al.*, 2005), the opportunities for such human-assisted interisland transport have been few. However, both tourist groups and research expeditions are

increasingly visiting more than a single island during a cruise (Frenot *et al*., 2005). In consequence, the probabilities of moving springtails around the region are growing. The present data therefore suggest that stringent quarantine procedures should be implemented when moving to, from, between, and, where feasible (especially when helicopter-assisted transport is used) within islands. The same argument would also apply to Antarctica, where recent, possibly human-assisted, transport of a springtail species among ice-free areas has already been documented (Stevens & Hogg, 2003), and where caution has been called for when moving between ice-free areas (Convey *et al*., 2000; Frenot *et al*., 2005). In the absence of such measures, molecular studies may well have to contend with distinguishing the signal of history from the noise of human movement patterns in the region.

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